JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 1997, **67,** 181–192 NUMBER 2 (MARCH)

LEARNING ABOUT FOOD: STARLINGS, SKINNER BOXES, AND EARTHWORMS

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Despite its importance as a tool for understanding a wide range of animal behavior, the study of reinforcement schedules in the laboratory has suffered from difficulties in the biological interpretation of its findings. This study is an operant-laboratory investigation of the ability of European starlings, *Sturnus vulgaris,* to learn to respond adaptively to the problem of foraging on patchily distributed prey that are uncertainly located in space. In order to maximize the biological relevance of the laboratory study, variation in the aggregation of earthworms, *Lumbricus terrestris* (a prey species), was rigorously quantified from the field, and the experimental birds were presented with reinforcement schedules designed to represent the extremes of the observed variation. The results demonstrate that, even for a single prey species, the degree to which individuals are aggregated can vary markedly over a range of spatial scales, and that starlings can rapidly learn to respond, in an adaptive manner, to these variations. These findings suggest that starlings are capable of adjusting their behavior to facilitate the efficient exploitation of prey that occurs in patches of an uncertain nature, and thus illustrate the heuristic value of an ecologically informed operant-laboratory approach to studying foraging behavior.

Key words: optimal foraging, reinforcement schedules, operant behavior, prey distribution, spatial aggregation, patchiness, *Sturnus vulgaris*

The study of reinforcement schedules in the laboratory has been widely used as a tool for understanding the behavior of foraging animals, both in investigations of biological function (e.g., testing optimal foraging theory) and psychological mechanism (see Shettleworth, 1988, for a review). Although such treatments have the advantage of precise control over many of the variables that are considered important for decision making when foraging (Hanson, 1987), the experimental procedures adopted have not always been easy to relate to the ecological problems faced by wild animals (e.g., Dallery & Baum, 1991; Fantino & Logan, 1979; Shettleworth, 1989). Recognition of this shortfall has contributed to a general increase in emphasis on the biological, or phylogenetic, determinants of behavior in the behavioral analysis literature over the last couple of decades (e.g., Fantino & Abarca, 1985; Fantino & Logan, 1979; Mellgren, 1982; Williams & Fantino, 1994).

Much of the progress towards addressing the problems with laboratory analogues of foraging behavior can be attributed to the adoption of a biologically informed approach to understanding behavior (e.g., Fantino & Logan, 1979). For the most part, this approach has involved integrating principles developed within psychology or behavioral analysis with theoretical frameworks developed in the behavioral ecology literature (e.g., the delay-reduction and optimal diet models of choice; Fantino & Abarca, 1985). In addition, gains have been made in developing laboratory tasks that are functionally similar to the foraging tasks that would be faced in the wild (e.g., Dallery & Baum, 1991; Mellgren, 1982). For example, Dallery and Baum demonstrated experimentally that the often-assumed equivalence of lever pressing and search effort in rats is justified, adding weight to assertions that search effort is best modeled using variable-ratio schedules (e.g., Hanson, 1987).

However, whether the theory being tested is biologically informed or not, significant scope still remains to increase the power of a laboratory-based approach to foraging behavior. Indeed, where an operant-laboratory ap-

Thanks to the Nuffield Foundation for financial support. Dall was funded by a Natural Environment Research Council, U.K., research studentship. We are also grateful to John Wixted and two anonymous referees for helpful comments on previous versions of this manuscript.

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proach is being used to test the predictions of optimal foraging theory, problems regarding the ecological relevance of the reinforcement schedules presented to the experimental subjects can still emerge. Mostly this will be a consequence of the theory being tested, because much optimal foraging theory deals with generalizations across ecological circumstance. As a result of this emphasis, schedules of reinforcement are often chosen more for their ability to illustrate general foraging phenomena than for their relevance to the experience of a specific organism in the wild. Indeed, Green (1987) asserts that this focus on generalities in the optimal foraging theory literature can underemphasize important phenomena that are considered special cases in these treatments. Instead he proposes a research program based primarily on "a knowledge of the ecological problem the [foraging] behavior is to solve" (Green, 1987, p. 290) for which specific mathematical models should be developed and tested using well-designed laboratory experiments that incorporate those ecological features that have been indicated as being important to the foraging animal. By investigating specific instances of general phenomena in such a way, the power of any laboratory manipulation, in terms of its ability to unambiguously manipulate key variables in a way that is relevant to the experimental subjects, can be increased substantially.

Following the above reasoning, the present study was designed to investigate the abilities of European starlings, *Sturnus vulgaris,* to cope with a laboratory analogue of an ecologically realistic foraging problem. The characteristics of the laboratory procedure were derived from detailed field data on the spatial distribution of potential prey. The specific problem investigated is that faced by starlings foraging for topsoil invertebrates (e.g., leatherjackets, Tipulidae; beetle larvae, Coleoptera; or earthworms, *Lumbricus terrestris*) on grazed pasture (Tinbergen, 1981; Wright & Cuthill, 1989). Because soil invertebrates (or indeed any organisms) are rarely distributed homogeneously in space due to biological interactions or variation in physical and chemical conditions (Pielou, 1977), efficient predators will be faced with the problem of locating and exploiting those areas of relatively high prey density. The efficient exploitation of these patches of prey has long been a focus for optimal foraging theory and much empirical work (reviewed by Stephens & Krebs, 1986), but the ability to locate such areas is rarely considered. When patches are obvious and can be located from a distance, such considerations are trivial. If, however, there are few or no cues to go by, and therefore their location is uncertain, finding patches will be fundamental to foraging efficiently. Such is the problem faced by starlings foraging for topsoil invertebrates.

There were two parts to the study described here. The first part was a field study to determine the type of scale over which a particular prey type (earthworms, *Lumbricus terrestris*) is aggregated on sheep pasture (measured in biologically relevant units). The second part consisted of a laboratory investigation of the ability of starlings to learn to exploit different schedules of reinforcement that were constructed to simulate scales of prey aggregation within the range observed in the field. In order to simulate the dependence of prey encounter on active searching, all the schedules of reinforcement were ratio based (Dallery & Baum, 1991; Hanson, 1987). The hypothesis that starlings are efficient foragers that can cope with variability of the sort found in the wild was tested. It was therefore predicted that the birds in the laboratory experiment should rapidly learn to respond efficiently when presented with schedules of reinforcement that simulated the extremes of the potential natural search-effort-prey-encounter contingencies.

METHOD

Field Study (Earthworm Aggregation)

Study site. Soil samples were obtained from two adjacent sheep pasture fields (total area, 2,024 hectares) at the University of Bristol Farm in Lower Langford, Avon, United Kingdom. They were collected in December 1994 and January 1995, during which period the site was ungrazed and the climatic conditions were fairly constant with moderate waterlogging of the fields. Starlings were observed to be foraging in these fields throughout the study period, both singly and in small flocks.

Procedure. Each soil sample was a cylinder approximately 4 cm in diameter and 5 cm in

depth; these values were chosen to approximate the volume of soil that is accessible to a starling when it probes for topsoil invertebrates (see Tinbergen, 1981, for a detailed description of this behavior). The sampling procedure was a modification of a design suggested by Oliver and Webster (1986) for efficient detection of spatial autocorrelation: the degree to which prey abundance at point x predicts that at point x'. A single replicate consists of a sample at a given point (the node) and a series of samples at different distances from the node. On any 1 day, node samples were obtained from eight randomly selected points in the study area. From each such node, samples were taken at six distances, each in a randomly selected direction; a single replicate thus consists of seven samples (one node plus six others). These distances were powers of 4 cm, chosen to approximate the step length of a starling. Any 1 day thus generated 56 samples (eight times seven samples) that were examined in the laboratory for the number of earthworms present within 24 hr of collection. Sampling was carried out on 5 different days to yield a total of 40 replicates and 280 samples. Thus, this sampling procedure (with samples at 4 cm, 16 cm, 64 cm, 256 cm, 1,024 cm, and 4,096 cm from each node sample) allowed us to determine the pattern of spatial correlation in earthworm numbers. What were the sign and strength of correlations between the number of prey at point y (the node) and the number found at increasing distances from y?

Earthworm numbers are discrete and liable to have a skewed distribution, so are not suitable for analysis by Pearson correlation. The procedure adopted was generalized linear interactive modeling using GLIM 4 (NAG Ltd., Oxford). GLIM has the advantage of allowing one to analyze data for which the unexplained, or error, variation is not normal, as is required for conventional parametric statistics. Two candidate error distributions were considered: Poisson and negative binomial. A Poisson distribution is appropriate for count data when each item (here, earthworm) is independently and randomly distributed. Conversely, the negative binomial distribution is often used to model count data that have clumped distributions, that is, when the probability of occurrence of an item is not independent of the others (Pielou, 1977). If earthworms aggregate together, or prefer substrates that are themselves clumped, then one might expect the negative binomial to provide a better fit than the Poisson. Negative binomial errors are not a standard option in GLIM, so we used the procedure recommended by Crawley (1995, pp. 339, 345–348) utilizing his supplied macro ''ownnb.mac.'' In the case of either Poisson or negative binomial models, the log link function was used to ensure that all fitted values are positive (otherwise the linear model might predict negative earthworm counts). Having specified the error distribution and link function, GLIM proceeds in a fashion similar to linear regression. However, the explanatory power of each x variable is expressed as a change in deviance rather than r^2. Changes in deviance are distributed approximately as chi-squared, with degrees of freedom equal to the change in degrees of freedom due to fitting the parameter of interest. Throughout we consider the number of worms at the node as the dependent variable and the number of worms at increasing distances as the predictor variables x_4, x_{16}, x_{64}, x_{256}, $x_{1,024}$ and $x_{4,096}$.

Laboratory Experiment

Subjects. Operant foraging trials were performed on 6 wild-caught juvenile female European starlings, *Sturnus vulgaris*. The birds had been captured during the previous summer and were housed, with other starlings, in an indoor free-flight room until the start of the training period. At this point they were housed together in two groups of 6. The subjects were selected from this pool of 12 randomly selected birds on the criterion of reaching asymptotic performance on the final training task (see below). This criterion was such that all birds could operate the manipulanda to obtain reinforcers, but none had experienced the experimental schedules. Throughout these periods the birds were maintained on long days (free-flight room, 13:11 hr light/dark; cages, 18:6 hr light/dark) and at a constant temperature (20 °C). Before and between trials, they had access to ad libitum food (turkey starter crumbs) and water (for bathing and drinking).

Apparatus. Prior to training, each bird was randomly assigned to one of six test cages in which all of the training and experimental trials were conducted. Within each cage was a

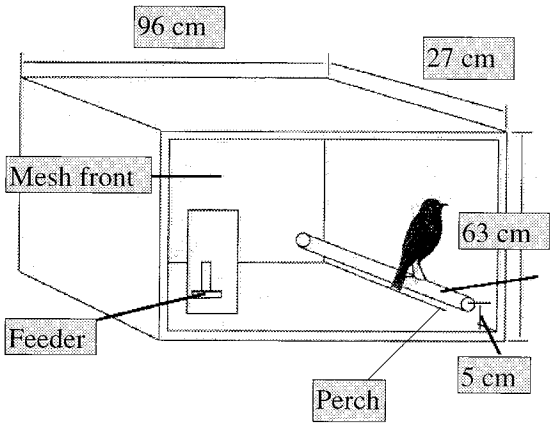

Fig. 1. Diagram of the operant cages (not drawn to scale).

feeder and drinking fountain at one end and an operant perch at the other (Figure 1). The feeder consisted of a small trough covered by a clear plastic door that could be pushed inwards to obtain the delivered reinforcer (0.05 g of turkey starter crumbs from a Campden Instruments Ltd. Model 442 food dispenser). This is the natural feeding action for starlings, achieved by inserting a closed bill and then opening it, similar to probing the topsoil for invertebrates (Tinbergen, 1981). In the terminology of behavioral ecology, the feeder and door unit comprises the patch. Both the probes at the feeder door and the hops on the perch could be detected as closures of microswitches, interfaced via a digital I/O board to a BBC Master computer running Spider software (Paul Fray Ltd., Cambridge, UK). The software also controlled the delivery of reinforcers according to various preprogrammed schedules.

Procedure. Prior to experimentation, the birds experienced training sessions individually in the operant cages. Each session, both training and experimental, began at 12 noon and lasted for 3 hr. First, after an initial session in which food was available from a plastic dish as well as from the trough, reinforcers were dispensed at random intervals of between 1 and 60 s with equal probability (a variable-time [VT] schedule with a mean interreinforcer time of 30 s; the intervals were drawn randomly from a rectangular distribution). At this stage of training, reinforcer delivery was not contingent upon probing, so reinforcers could accumulate in the trough, but all birds had to probe at the feeder door in order to remove reinforcers. After all the birds demonstrated that they were eating from the feeders (indicated by empty or nearly empty troughs at the end of a session), the delivery of a reinforcer was made contingent upon on the bird hopping on the perch, with hops being continuously reinforced (fixed-ratio [FR] 1). When the birds had reached a steady state of hopping and probing (indicated by the total number of events per session), the programmed schedule was changed such that three hops switched on the feeder light, at which point a reinforcer could be obtained after a probe at the feeder door (chained FR 3 hops on perch, FR 1 probes at feeder door). After a reinforcer was delivered, the light was extinguished and another three hops on the perch were required before feeder (patch) availability was cued again. The final training phase was initiated when the total number of reinforcers gained per session stopped increasing. This final training phase involved the delivery of a reinforcer only after two probes at the feeder door. Thus, training ensured that a combination of probing at the feeder and hopping on the perch was shaped (i.e., chained FR 3 hops, FR 2 probes), with reinforcement available only in the final probe link of the schedule.

Prior to the first experimental session the birds were randomly assigned to two equal groups that differed in the order in which the treatment schedules were experienced (a repeated measures design). There were two such schedules, called here dispersed and clumped, that varied according to the relative degree of prey aggregation they were designed to simulate. For both schedules the birds could either probe continuously or perform a combination of hops and probes for reinforcement (Figure 2). The schedules were designed such that one hop was the response equivalent of 10 probes, so performing a combination of tasks would be more efficient (in terms of minimizing the number of responses to reinforcement) than just probing. As with the final training schedules, however, only the final probe in the chain schedule could be directly reinforced. For the dispersed treatment, a reinforcer was delivered on the first probe after either 10 probes or one hop. Any subsequent probes were not reinforced until the above minimum re-

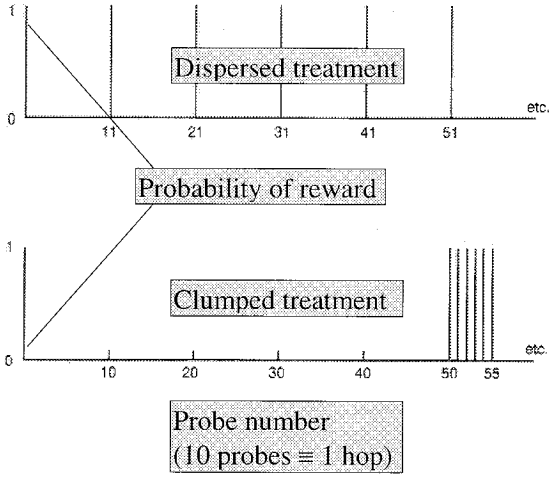

Fig. 2. Diagrams to illustrate the reinforcement schedules for each of the two treatments.

sponses (10 probes or one hop) had been performed again. In contrast, the clumped treatment required that the subject probe 50 times or hop at least five times (or any combination of hops and probes equivalent to at least 50 probes) before the next five probes would be reinforced. After the fifth reinforced probe, subsequent probes were not reinforced until the next clump of reinforcers was reached (see Figure 2 for summary). This is a chained FR 50 FR 1, with a limit of five reinforcers obtainable on the final FR 1 link. For both treatments the occurrence of the patches of reinforcers was uncued, and birds could not overrun patches (more responses than the minimum requirement were not penalized).

The schedules were similar to those designed by Williams and Fantino (1994), who presented pigeons with single versus clustered encounters in a concurrent-chains procedure. Thus, similar to their single encounter option, in our dispersed treatment, an initial FR link (FR 10 probes or FR 1 hop) led to a single terminal FR 1 probe link. In our clumped treatment, as in Williams and Fantino's clustered encounters option, an initial FR link (FR 50 probes, FR 5 hops, or any combination of hops and probes equivalent to at least 50 probes given that one hop ≡ 10 probes) led to successive FR 1 probe links (in our case five such links). The differences between our treatments and those of Williams and Fantino are that none of the links in any treatment schedule were cued (designed to simulate foraging on a relatively homogenous substrate), the subjects had alternative choices as to how to complete their initial-link schedules, and the two treatments were not presented concurrently.

The operant tasks and reinforcement schedules were designed to simulate the response–reinforcement contingencies encountered by a starling foraging on grazed pasture as closely as possible. When probe foraging, starlings can move forward slowly by probing continuously, or alternate bouts of probing with bounds or short walks (Feare, 1984; Tinbergen, 1981). In our experiment then, hops were equivalent to walking or bounding, which allowed the subject to progress relatively rapidly through the simulated foraging space. Only by probing, however, can prey be encountered by a starling foraging on topsoil invertebrates, so only probes were directly reinforced. In addition, the schedules of reinforcement allowed the subjects the option of continuously probing their way through foraging space, a more laborious alternative that is also available to starlings in the wild. The different treatment schedules were designed to simulate a change in the degree of aggregation from prey every step to prey every five steps without changing the overall mean density of prey items.

If starlings can learn to forage efficiently in our laboratory simulation, then it was predicted that they should rapidly adjust their behavior so as to minimize response effort to reinforcement. The experimental period lasted for 12 sessions (one per day), with the change of schedules occurring after the sixth session. Given the day-to-day unpredictability of their natural environment and the length of foraging time available to a starling in a day, it was reasoned that efficient starlings should be able to learn to behave effectively within the six 3-hr sessions that were allowed in the experiment.

We recorded a range of behavioral variables for each bird in each session. Because there are several dependent variables to be analyzed, multiple independent testing would have inflated the Type I error rate. In addition, because many of the dependent variables to be analyzed are correlated, all variables were first entered into multivariate ANOVA (MANOVA; SPSS Inc., 1990). As is

Table 1

GLIM results with the number of earthworms in the node sample as the dependent variable. Error variance is negative binomial (see text).

Fitted parameter	Δdeviance	Δ*df*	*p* value
x_4	7.511	1	<.01
x_{16}	1.317	1	*ns*
x_{64}	9.697	1	<.01
x_{256}	0.888	1	*ns*
$x_{1,024}$	0.039	1	*ns*
$x_{4,096}$	0.001	1	*ns*

Note. ns refers to any *p* value greater than .05 (i.e., not significant).

appropriate for a repeated measures design, in both multivariate and univariate ANOVA all independent variables were treated as fixed effects and subject as a random effect (mixed-model design; Howell, 1992). The independent variables were treatment (dispersed or clumped), order (dispersed on Sessions 1 to 6 then clumped on Sessions 7 to 12, or vice versa), and session (1 to 6, within treatment). For clarity, only the appropriate univariate *F* ratios are presented.

RESULTS

Field Study (Earthworm Distribution)

Before testing correlations with earthworm numbers at different distances from the nodes, the effect of day-to-day variation in mean numbers was investigated by fitting the factor day (with five levels corresponding to the different sampling days). With Poisson error, there was a large residual deviance (54.475, $df = 39$). This indicates overdispersion (Crawley, 1995, p. 347) so we fitted a negative binomial error. The lower residual deviance (52.95, $df = 39$) indicates a better fit; subsequently, day was fitted and did not have a significant effect (Δdeviance = 5.547, $\Delta df = 4$, $p > 0.05$). All further models therefore only involved negative binomial error. Table 1 displays the change in deviance through fitting each of the variates x_4 to $x_{4,096}$ separately. The number of earthworms at the node is correlated significantly and positively with the number at 4 cm distant, and is correlated significantly and negatively with the number 64 cm distant. Moreover, the pattern of correlations, at increasing distances from the node, shows this as a progressive switch from positive to negative, to zero, correlation (Figure 3).

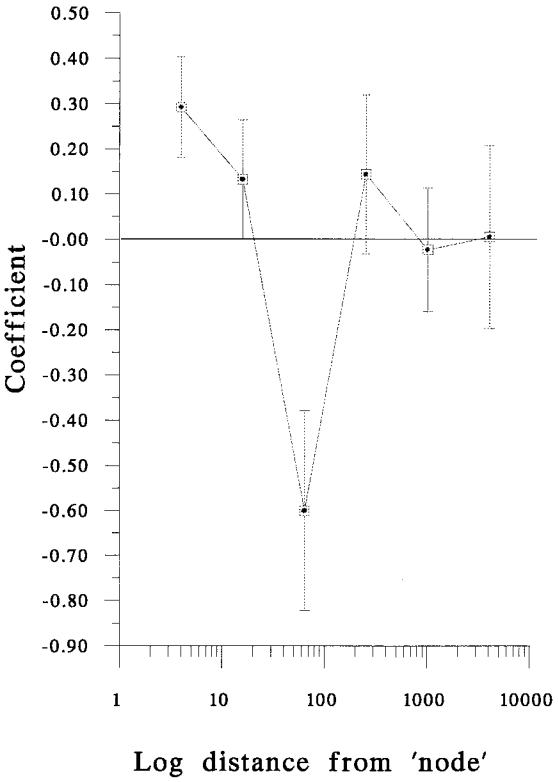

Fig. 3. A plot of the coefficient of the relationship between the number of earthworms at each of the distances from the node (in centimeters) and the number of earthworms at the node against the log of those sample distances. The solid line represents no relationship between the variables (coefficient = 0). The coefficients were obtained from the GLIM analysis described in the text.

Laboratory Experiment

There is a significant three-way Treatment × Order × Session interaction for both the number of probes, $F(5, 20) = 13.43$, $p < .001$, and number of hops, $F(5, 20) = 211.13$, $p < .001$, per session. As can be seen in Figure 4 (a and b), this is due to an effect of order, but not treatment, on Sessions 1 and 7, and an effect of treatment, but not order, on subsequent sessions: The ANOVA on Sessions 1 and 7 alone showed no significant effects of treatment for probes, $F(1, 4) = 2.09$, $p = .222$, and hops, $F(1, 4) = 0.232$, $p = .232$; significant effects of order, probes $F(1, 4) = 298.96$, $p < .001$, hops, $F(1, 4) = 752.81$, $p <$

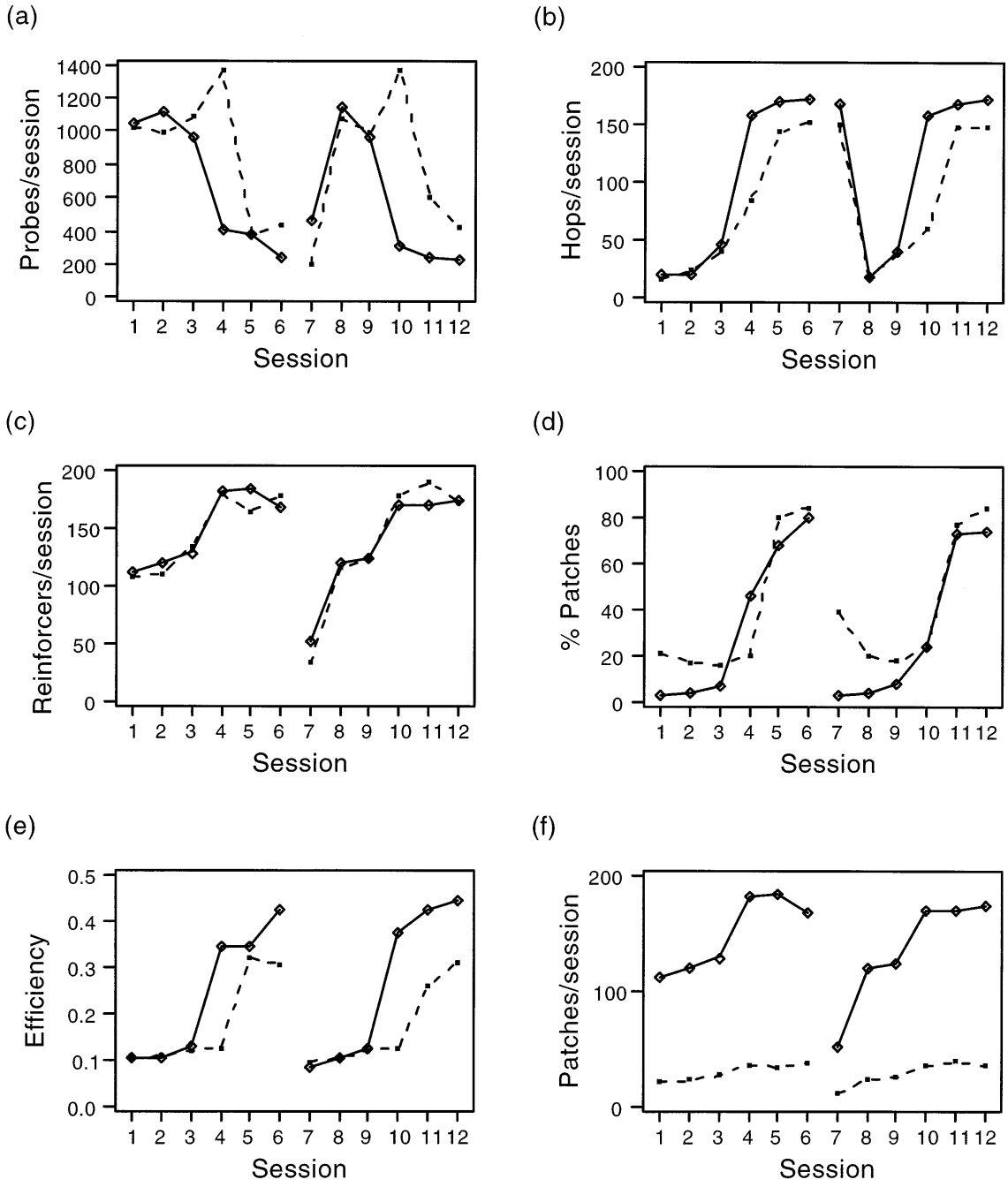

Fig. 4. The behavior and performance of the starlings experiencing the different schedules in different orders (solid line and diamonds: dispersed treatment; dashed line and squares: clumped treatment). Each point is the mean of 3 subjects (see Appendix for individual data). Note that the treatments were switched for each group of 3 subjects after Session 6, such that half the subjects experienced the dispersed treatment in Sessions 1 to 6 and the clumped treatment in Sessions 7 to 12, whereas the other half experienced the clumped treatment in Sessions 1 to 6 and the dispersed treatment in Sessions 7 to 12. (a) The mean number of probes performed per session, (b) the mean number of hops per session, (c) the mean number of reinforcers obtained per session, (d) percentage of patches in which a hop (as opposed to a probe) followed the final reinforcer in a patch, (e) the mean efficiency (reinforcers/[hops + probes]) per session, and (f) the mean number of patches visited per session (see text).

.001; no significant Treatment × Order interactions for probes, $F(1, 4) = 0.17$, $p = .945$, hops, $F(1, 4) = 1.00$, $p = .374$. Birds at the start of the experiment, regardless of treatment, probed a lot but hopped little; however, birds on the changeover day between treatments (Session 7) hopped a lot but probed little (compare the behavior of the birds in both treatments for Session 1 vs. Session 7 in Figure 4a and b). This high hopping and low probing rate, for those birds switching to a new treatment, was a carryover effect from their response pattern at the end of the previous treatment. Regardless of order and treatment, from the second through the sixth session in each treatment block (Sessions 2 to 6 and 8 to 12) there was a progressive decline in probing and an increase in hopping, suggesting that the birds were learning that hopping was more efficient than probing for gaining access to patches of reinforcers (i.e., fewer operant responses per reinforcer are required). However, these behavioral adjustments occurred more rapidly for subjects in the dispersed treatment than for those in the clumped treatment (Figure 4a and b). The ANOVA on Sessions 2 to 6 and 8 to 12 showed a significant Session × Treatment interaction for probes, $F(1, 4) = 25.06$, $p < .001$, and hops, $F(1, 4) = 102.41$, $p < .001$, but no significant Treatment × Order × Session interactions for either, $F(1, 4) = 0.38$, $p = .817$ and $F(1, 4) = 2.21$, $p = .114$, respectively. The high rate of probing on a novel reinforcement schedule is not surprising, because it is only by probing that the birds can experience the aggregation of prey within patches. Thus, birds at the start of the experiment (Session 1) probed a lot and, after one session's experience in which they could have detected that the distribution of prey had changed (after Session 7), their rates of probing increased to levels similar to those at the start of the experiment (compare Session 8 with Session 1 in Figure 4a and b).

The net effect of the switch from high levels of probing to increased hopping is, as one might expect, to increase the numbers of reinforcers gained per session (Figure 4c). One hop is worth 10 probes in terms of what might be called "travel" to a new patch, so this change in behavior is more efficient along the dimension of the number of reinforcers per response. An ANOVA on reinforcers showed a significant Treatment × Order × Session interaction, $F(5, 20) = 13.03$, $p < .001$. Inspection of Figure 4c suggests that this interaction is due to a difference between Sessions 1 and 7. Birds experiencing a new patch type on the changeover session (Session 7) showed depressed reinforcement gain rates: The ANOVA on Sessions 1 and 7 alone showed no significant treatment effect, $F(1, 4) = 1.35$, $p = .310$, a significant order effect, $F(1, 4) = 69.79$, $p = .001$, and no significant Treatment × Order interaction, $F(1, 4) = 0.46$, $p = .535$. Thereafter both treatments and both orders were associated with similar increases in reinforcers gained per session. The ANOVA on Sessions 2 to 6 and 8 to 12 showed the following: session, $F(1, 4) = 63.65$, $p < .001$, treatment, $F(1, 4) = 0.02$, $p = .901$, order, $F(1, 4) = 1.37$, $p = .307$; all interaction terms $p > .19$.

The daily increase in hopping, at the expense of probing, presumably occurred because prey occurred singly in the dispersed treatment and in groups of five in the clumped treatment. A reinforced probe in the dispersed treatment could come to signal that no further prey are immediately forthcoming, so it is best to hop (once) before returning to the patch. A reinforced probe in the clumped treatment likewise could come to signal that four further probes will each be reinforced, but that after the fifth reinforcer it is best to hop (five times) before returning to the patch. That birds learn based on these contingencies, in both treatments and orders, is suggested by an analysis of the proportion of operant responses that were hops, rather than probes, following completion of a patch (i.e., after one reinforcer in the dispersed treatment or after five reinforcers in the clumped treatment). For all birds (see the Appendix for responses of individual birds) the percentage of hopping after a patch increased (Figure 4d): significant factor session, $F(5, 20) = 101.4$, $p < .001$; but there were treatment differences in the pattern of increase: significant Treatment × Session interaction, $F(5, 20) = 4.79$, $p = .005$. Birds in the clumped treatment showed higher tendencies to hop after a patch for the first two sessions, but the treatment differences disappeared thereafter when birds in both treatments showed similar daily increases: Separate ANOVAs were conducted for each

session within treatment, factor treatment, Sessions 1 and 7, $F(1, 4) = 7.89$, $p = .049$; Sessions 2 and 8, $F(1, 4) = 499.51$, $p < .001$; Sessions 3 and 9, $F(1, 4) = 7.40$, $p = .053$; Sessions 4 and 10, $F(1, 4) = 3.49$, $p = .135$; Sessions 5 and 11, $F(1, 4) = 4.24$, $p = .109$; Sessions 6 and 12, $F(1, 4) = 7.08$, $p = .056$; factors order and Treatment × Order all $p > .10$.

That birds adjusted to the nature of each resource distribution was revealed in the daily increase in hopping after the requisite number of reinforcers per patch. These changes resulted in greater foraging returns per unit effort (reinforcers per operant response). The increased number of reinforcers per session has already been described, but there is also a between-session increase in number of reinforcers per response. This measure of foraging efficiency (reinforcers/[hops + probes]) would be .5 for a bird that responded perfectly in either treatment: In the dispersed treatment, birds should probe and hop alternately to gain the maximum number of reinforcers in the minimum time and effort (efficiency = 1 reinforcer/[1 hop + 1 probe] per cycle); in the clumped treatment they should probe five times successively to empty a patch, then hop five times in a row to find the next patch (efficiency = 5 reinforcers/[5 hops + 5 probes] per cycle). An ANOVA on efficiency showed an increase with successive sessions for both treatments irrespective of order (Figure 4e); factor session, $F(5, 20) = 148.3$, $p < .001$, all factors involving order were not significant. From Sessions 4 and 10 onwards, birds in the dispersed treatment performed better on this criterion, approaching the perfect ratio of .5. Birds in the clumped treatment also improved, but more slowly, and they reached a lower maximum level (Figure 4e): Separate ANOVAs were conducted for each session, factor treatment, Sessions 1 and 7, $F(1, 4) = 0.14$, $p = .723$; Sessions 2 and 8, $F(1, 4) = 1.25$, $p = .327$; Sessions 3 and 9, $F(1, 4) = 1.63$, $p = .271$; Sessions 4 and 10, $F(1, 4) = 45.56$, $p = .003$; Sessions 5 and 11, $F(1, 4) = 7.64$, $p = .051$; Sessions 6 and 12, $F(1, 4) = 149.42$, $p < .001$. The changes in foraging efficiency also resulted in a greater total number of patches being visited per trial with, as one might expect, relatively more patches being visited in the dispersed treatment (Figure 4f); factor treatment, $F(1, 4) = 237.06$, $p < .001$, session, $F(5, 20) = 148.3$, $p < .001$, Treatment × Session, $F(5, 20) = 16.78$, $p < .001$; all factors involving order were not significant. By Sessions 6 and 12 the ratio of patches visited per trial in the dispersed treatment to those visited in the clumped treatment was not significantly different from the expected value of 5: $M = 4.739$, $SE = 0.203$, paired $t(5) = 1.28$, $p = .260$.

DISCUSSION

There are a number of points that emerge from the results presented here. First, the results of the field sampling study indicate that, even for a single prey species, the degree to which individuals are aggregated can vary markedly over a range of spatial scales. The degree to which the number of earthworms found at each of the nonnode samples correlates with the numbers found at the corresponding node varies in both sign and significance. Thus, within approximately one step length (4 cm) after finding an earthworm, our results indicate that a foraging starling is likely to find more prey. However, if a bird walks about 16 steps (64 cm) after finding a prey item, then a probe will likely be unsuccessful. Likewise, if a probe is unsuccessful, then probing within one step length is likely to be unproductive, whereas probing after 16 steps should be productive. At intermediate (and greater) distances, however, the number of prey already found does not predict potential foraging success. This biologically relevant measure of the spatial distribution of potential prey is only possible with explicit reference to the predator involved and has important implications for the variance in encounter rate that is likely to be experienced. This will determine the best search-and-exploit strategy to use. For the purpose of this study, it is significant only that patchiness over a scale that is potentially detectable by a foraging starling has been demonstrated.

At the scale of single probes (within the 4-cm diameter of the core) or one step length (cores 4 cm away), earthworms are clumped. Their numbers are well fitted by a negative binomial distribution, indicating overdispersion, and numbers in nearby cores are positively correlated. However, these patches are themselves somewhat regularly distributed, as

indicated by the negative correlation between numbers in cores at intermediate (64 cm) distances. The mechanism that generates this regular pattern of earthworm patches is unknown, but a plausible candidate is the remnant of past ploughing, creating regular ridges and furrows at this sort of spatial scale. Such areas of greater and lesser waterlogging are liable to affect earthworm distributions, but at present this mechanism is speculative. The significance of pattern generated by environmental regularities, rather than, say, earthworm–earthworm interactions, is that starlings could use such microgeographic variations as secondary cues to earthworm distribution. Whether they do so remains to be ascertained.

It was predicted that starlings should be able to rapidly adapt their foraging behavior to the type of change in spatial aggregation demonstrated by their prey species. The starlings in our study were presented with reinforcement schedules designed to simulate the extremes of earthworm aggregation that would be encountered in the wild; in other words, those situations in which a reinforced probe would guarantee that the next few probes would also be reinforced (clumped treatment) versus situations in which a reinforced probe predicts that the next few probes would not be reinforced (dispersed treatment). In fact, the birds came to respond efficiently under the different treatments in a relatively short period of time (maximum of 5 days). This flexibility was adaptive in the context of the schedules used, and, for both treatments, asymptotic performance was close to perfect (in terms of minimizing the number of responses to reinforcement). The birds performed slightly more efficiently in the dispersed treatment (see Figure 4e). These results have implications for understanding both the mechanisms by which birds respond to differences in prey distribution and the adaptive significance of this behavior.

At asymptotic performance, the behavioral strategies (or rules) would have to be different under the different reward schedules. For the dispersed treatment a simple win-shift rule (e.g., Olton & Schlosberg, 1978) would suffice, but for the clumped treatment a more complex rule would be required. For example, the latter could involve some modified version of a win-stay rule that involved counting the number of successful attempts and leaving the patch after receiving the fifth. The starlings were not just simply win-staying lose-shifting in the clumped treatment, because relatively little overprobing was observed (see Figure 4d). It is perhaps not surprising, then, that performances were relatively more efficient on the dispersed schedule, because the more complex the behavioral strategy (rule) required, the more difficult it will be to perform. For example, having to count to five on the clumped schedule would be more prone to error than having to switch based solely on the last response.

On the functional (adaptive) side, our findings reveal little about the currency controlling starling foraging behavior that relates the short-term consequences of their actions (e.g., how much energy is obtained and at what cost) to their fitness on an evolutionary time scale (see Houston & McNamara, 1989, and Maynard Smith, 1978, for discussions). This is because the optimal responses to both of the treatments presented are to use fixed-number strategies (i.e., move on after finding a certain number of prey) that differ only in the number of prey that are expected (one vs. five). Such strategies can be optimal under a range of currencies, including maximizing the net rate of energy intake, minimizing the risk of an energy shortfall, and maximizing energy efficiency, to name but a few. Nevertheless, this study has important implications for the ability of starlings to exploit patchy prey types in general because it demonstrates flexible learning of the extremes of the reinforcement schedules (ratio based) that will be encountered when foraging for such prey.

The fact that the starlings in our study were able to respond appropriately under simulations of contrasting correlations between prior success and the success of future foraging attempts implies that the mechanisms necessary for the efficient exploitation of clumped prey are available. The efficient exploitation of such resources requires the behavior of foragers to be responsive both to negative and positive correlations between past and future success. For example, foragers on the earthworms that were sampled here must learn to travel some distance following failure (e.g., by bounding or flying rather than walking) but not following a success. Conversely, when walking, foraging starlings should

probe close by following a success but not following failure. The starlings in our study demonstrated the ability to behave differently and appropriately under these types of reinforcement schedules. Our results therefore indicate that European starlings, *Sturnus vulgaris,* possess the attributes required for the efficient exploitation of aggregated prey when patches are not detectable without sampling. This type of spatial distribution is expected for topsoil invertebrates that are sensitive to the varying physical and chemical conditions of the soil, and is observed here for earthworms, *Lumbricus terrestris,* living in sheep pasture.

The approach taken here was to design both the operant tasks to be performed and the reinforcement schedules presented with explicit reference to a realistic foraging problem faced by starlings in the wild. On the ecological sampling side, the explicit reference to a spatial scale that is appropriate to foraging starlings has allowed an ecologically relevant foraging problem to be characterized with a high degree of precision. This, along with careful attention to the details of the appropriate foraging strategy employed by starlings in the wild, has allowed the relevant reinforcement schedules to be designed. Such an approach can both complement and increase the power of the current biologically informed approach to laboratory manipulations advocated by modern behavior analysts (e.g., Fantino & Logan, 1979). In conclusion, combining the precision of experimental psychology and optimal foraging theory with the external validity of field ecology should lead to an improved understanding of foraging behavior.

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Received July 8, 1996
Final acceptance October 23, 1996

APPENDIX

Data for individual subjects. Subjects 1, 4, and 5 experienced treatments in the order clumped then dispersed; Subjects 2, 3, and 6 experienced dispersed then clumped.

Dependent variable	Treatment	Session	Subject 1	2	3	4	5	6
Probes per session	Dispersed	1	497.0	1,141.0	1,175.0	390.0	502.0	832.0
		2	1,268.0	1,129.0	1,067.0	1,239.0	945.0	1,153.0
		3	987.0	1,006.0	740.0	791.0	1,135.0	1,161.0
		4	261.0	205.0	370.0	404.0	258.0	660.0
		5	196.0	402.0	535.0	325.0	200.0	210.0
		6	191.0	322.0	182.0	236.0	239.0	195.0
	Clumped	1	1,085.0	192.0	198.0	830.0	1,168.0	192.0
		2	958.0	890.0	1,151.0	1,029.0	975.0	1,205.0
		3	842.0	1,003.0	1,001.0	1,115.0	1,306.0	969.0
		4	1,425.0	1,305.0	1,340.0	1,569.0	1,104.0	1,460.0
		5	325.0	593.0	460.0	384.0	404.0	758.0
		6	520.0	351.0	369.0	332.0	454.0	538.0
Hops per session	Dispersed	1	151.00	19.00	20.00	172.00	184.00	18.00
		2	14.00	18.00	22.00	18.00	21.00	20.00
		3	41.00	49.00	47.00	43.00	35.00	39.00
		4	151.00	161.00	161.00	162.00	159.00	154.00
		5	174.00	171.00	161.00	160.00	168.00	177.00
		6	175.00	168.00	173.00	170.00	173.00	173.00
	Clumped	1	18.00	151.00	165.00	16.00	13.00	132.00
		2	23.00	21.00	18.00	28.00	18.00	17.00
		3	39.00	35.00	33.00	48.00	30.00	45.00
		4	88.00	51.00	64.00	91.00	70.00	63.00
		5	149.00	153.00	152.00	142.00	140.00	142.00
		6	157.00	142.00	149.00	145.00	157.00	153.00
Reinforcers per session	Dispersed	1	35.00	121.00	125.00	76.00	45.00	92.00
		2	128.00	119.00	117.00	129.00	105.00	123.00
		3	127.00	136.00	110.00	111.00	135.00	141.00
		4	161.00	165.00	180.00	184.00	168.00	200.00
		5	176.00	192.00	195.00	175.00	161.00	164.00
		6	170.00	182.00	165.00	176.00	179.00	160.00
	Clumped	1	115.00	33.00	37.00	90.00	118.00	29.00
		2	108.00	100.00	121.00	119.00	105.00	125.00
		3	112.00	123.00	121.00	145.00	146.00	129.00
		4	185.00	165.00	180.00	189.00	164.00	190.00
		5	165.00	193.00	180.00	164.00	164.00	198.00
		6	190.00	161.00	169.00	162.00	184.00	188.00
Percentage of patches in which a hop followed the final reinforcer in a patch	Dispersed	1	0.000	2.479	3.200	7.895	0.000	4.348
		2	3.125	3.361	5.983	3.876	3.810	4.065
		3	7.087	5.882	7.273	9.910	5.926	6.383
		4	9.317	49.091	47.222	13.043	50.000	42.000
		5	71.023	64.062	63.590	70.857	76.398	75.610
		6	82.941	79.670	87.879	75.568	62.011	71.875
	Clumped	1	13.043	50.000	66.667	33.333	17.391	0.000
		2	14.286	20.000	20.833	17.391	19.048	20.000
		3	27.273	12.500	16.667	10.345	10.345	24.000
		4	18.919	21.212	27.778	18.919	21.875	21.053
		5	84.848	78.947	80.556	62.500	93.750	71.795
		6	78.947	84.375	87.879	93.750	80.556	81.081
Patches per session	Dispersed	1	35.00	121.00	125.00	76.00	45.00	92.00
		2	128.00	119.00	117.00	129.00	105.00	123.00
		3	127.00	136.00	110.00	111.00	135.00	141.00
		4	161.00	165.00	180.00	184.00	168.00	200.00
		5	176.00	192.00	195.00	175.00	161.00	164.00
		6	170.00	182.00	165.00	176.00	179.00	160.00
	Clumped	1	23.00	9.00	14.00	18.00	24.00	15.00
		2	22.00	20.00	25.00	26.00	21.00	25.00
		3	23.00	26.00	25.00	29.00	30.00	28.00
		4	37.00	33.00	36.00	39.00	34.00	38.00
		5	33.00	40.00	36.00	36.00	35.00	41.00
		6	38.00	33.00	36.00	34.00	40.00	38.00